THE LATITUDINAL COMPENSATION HYPOTHESIS: GROWTH DATA AND A MODEL OF LATITUDINAL GROWTH DIFFERENTIATION BASED UPON ENERGY BUDGETS. I. INTERSPECIFIC COMPARISON OF *OPHRYOTROCHA* (POLYCHAETA: DORVILLEIDAE)

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ABSTRACT

A northern (North Carolina) sibling species of *Ophryotrocha* grew more rapidly than a southern sibling species (Florida); this presumed advantage, however, diminished to zero as temperature increased from 15 to 30°C. Survival of the northern sibling species was low at 30°C. The differential response probably had a genetic basis since both species had been reared for 2–3 generations under the same conditions. The effect lasted in laboratory populations reared for a year in the laboratory at 25°C (*ca.* 10 generations).

My results are consistent with a graphical model that suggests an evolutionary shift of metabolism-temperature curves and feeding efficiency curves for the two sibling species. These shifts predict a changing advantage of growth of one species relative to the other as temperature increases.

INTRODUCTION

Many studies have demonstrated physiological differences among latitudinally separated or otherwise thermally disparate populations of the same species or among closely related species. Differentiation has been recorded for metabolic rate (Mangum, 1963), temperature tolerance (Zhirmunsky, 1959), egg development time (McLaren *et al.*, 1969) and spawning temperature (Loosanoff and Nomejko, 1951). Krogh (1916) predicted that such differences should be consistent with a compensatory adaptation to maximize growth rates in a given temperature regime. Animals living in low temperature (high latitude) locales would thus be expected to "compensate" by increasing metabolic and growth rates at a given temperature, relative to animals from high temperature (low latitude) locales. This difference would be analogous to the seasonal adjustment of Q_{10} found in many marine invertebrate species. Winter-acclimated animals can sustain more activity than summer animals maintained at the same low temperature (see Kinne, 1964; Newell, 1973 for literature summaries and general discussion).

An appropriate physiological compensation for latitudinal position occurs for many, but not all, examined species. Scholander *et al.* (1953) found compensatory metabolism-temperature (M-T) adaptation in a comparison of arctic and tropical poikilotherms. Compensatory differences occur for latitudinally separated populations of a single species. Heart-beat rate, water propulsion speed, somatic growth rate, and oxygen consumption rate differ among populations of the mussel *Mytilus californianus* on the west coast of North America (*e.g.*, Rao, 1953; Dehnel, 1956; Pickens, 1965). In cases of compensation, high latitude populations show an upwards displacement

of the M-T curves relative to low latitude populations. This form of compensation is not universally observed, however (*e.g.*, Fox, 1936; Vernberg and Vernberg, 1966).

There are two generalizations from studies on latitudinal variation in growth rates. Individuals of high latitude populations of poikilotherms often obtain larger maximum body size than conspecifics or closely related species living at low latitudes (*e.g.*, Weymouth and McMillan, 1931; Ray, 1960). Secondly, although cold temperatures often reduce activity and constrain individuals to grow more slowly, they compensate by accelerating growth rate or larval development rate, relative to low latitude-derived individuals, when both are reared at the same temperature (Schneider, 1967; Ament, 1979; Bervan *et al.*, 1979).

Although adaptation to low temperature would probably entail a form of compensation involving relative acceleration of growth of the high latitude form at low temperature, one might expect that this shift in metabolism would result in an increased cost at higher temperature, leaving these forms at an energetic disadvantage in higher temperature environments. In other words, "latitudinal compensation" may not be compensation at all. Rather, local populations may shift their metabolic properties to maximize growth under local temperature conditions. A manifestation of this shift is a presumed acceleration of forms living in low temperatures, relative to high temperature forms reared at the same temperature. This shift would be either in the form of local evolution, or non-genetic response such as acclimation.

It is the purpose of this paper to present evidence for genetically based differences in somatic growth rates among latitudinally separated sibling species of *Ophryotrocha* (Polychaeta; Dorvilleidae). A companion paper will demonstrate differences between subspecies. I will propose a model based upon energy budgets to explain latitudinal clines in growth rate and body size in marine poikilotherms. The model assumes that all populations evolve to maximize growth rate; observations of acceleration are merely a manifestation of this selection pressure.

Evidence for genetically-based physiological compensation

Latitudinal differences in allozyme variants occur in a wide variety of invertebrates and fishes (*e.g.*, O'Gower and Nicol, 1968; Johnson and Utter, 1973; Williams *et al.*, 1973; Koehn *et al.*, 1976). Although this clinal variation is obviously correlated with temperature change, it is not clear that the genetic differences account for the physiological differences observed in the studies cited above. In the mussel, *Mytilus edulis*, extensive latitudinal differentiation in allele frequencies occurs on the east coast of North America. By contrast, little differentiation is found in *M. californianus* along the west coast. This correlates well with the steep latitudinal thermal gradient on the east coast as opposed to the gentle gradient on the west coast (Levinton and Suchanek, 1978). Heat-stable variants of the enzyme phosphoglucomutase are more common in more southern relative to northern populations of the east coast ribbed mussel *Geukensia demissus* (Gosling, 1979). Thus physiological differentiation may be genetically based. Adaptation at the molecular level has been shown between species living in different environments (*e.g.*, Somero and DeVries, 1967; Hochachka and Somero, 1973; and references therein) and some evidence exists for adaptive enzyme variants within a marine invertebrate species (Burton and Feldman, 1983; Hall, 1983; Koehn *et al.*, 1980).

Latitudinal differences in whole-animal physiological parameters may or may not have a genetic basis. There are three possible components of physiological response (Kinne, 1962). (1) Labile Compensation: individuals differ physiologically due to local acclimatization. These differences are reversible after a period of laboratory

acclimation (*e.g.,* Pickens, 1965). (2) Irreversible Non-genetic Compensation: field conditions induce irreversible physiological changes that cannot be eliminated through laboratory acclimation (*e.g.,* Gibson, 1954; Zamer and Mangum, 1979). These differences are acquired independently of genotype; irreversible effects are fixed because of the environment only. An obvious example is temperature-induced sex in fishes (*e.g.,* Conover and Kynard, 1981). (3) Genetically-based Physiological Differences: this is difficult to distinguish in the field from irreversible non-genetic compensation. An irreversible physiological response could result from irreversible non-genetic, or genetically-based responses (*e.g.,* Levinton and Lassen, 1978). Unfortunately, it is not possible to distinguish between these two alternatives in most studies demonstrating differences among field-collected adults. A useful approach would be the examination of progeny of populations that have been reared in the laboratory under identical conditions, preferably for several generations (*e.g.,* Battaglia, 1957; Schneider, 1967; Ament, 1979). The examination of progeny of laboratory-reared stocks, however, may involve unrealistic laboratory conditions and ignoring field parameters that might affect gene expression. Despite these potential problems, I take the latter approach in this study.

MATERIALS AND METHODS

Three populations of two sibling species of *Ophryotrocha* (Polychaeta; Dorvilleidae) were collected. *Ophryotrocha* species are found commonly in microhabitats of fouling communities, and are readily cultured in the laboratory (*e.g.,* see Akesson, 1976, 1978; Sella, 1978). *O. costlowi* Akesson was collected from Morehead City, North Carolina, and *O. macrovifera* Akesson was collected from Tampa Bay, Florida and at St. Lucie's Inlet, Florida. Identifications were confirmed via crossing tests performed by Prof. Bertil Akesson, Goteborg University. Initial populations of approximately fifty individuals were reared on ground, par-boiled spinach, at room temperature (20°C) and 30‰ salinity. Sea water used for culture was twice glass-fiber filtered, sterilized for 24 hours at 80°C, and cooled to room temperature. Worms were cultured in glass evaporating dishes, whose curved sides permit easy examination of worms and egg cases under the dissecting microscope at 12–50× magnification.

Both species belong to the "labronica" group of *Ophryotrocha* (Akesson, 1978). Sexes are separate and the male follows the female for some time (hours to over a day) before sperm is transferred. Females construct a tubular egg mass and reside in the tube until juveniles develop directly and emerge from the egg case. The near simultaneous emergence permits experiments with large numbers of siblings of identical age to be initiated at the same time.

Somatic growth rates were measured in two ways. First, animals were collected in the field and held at *ca.* 20°C (approximately 2 degrees variation) for 2–3 generations. Approximately twenty newly emerged juveniles from the same family were placed in a dish with spinach. Individuals were transferred to constant temperature environmental chambers held at 15, 20, 25, or 30°C (variation was less than 0.5°C). Reciprocal transplants from different pairs of temperatures demonstrated no significant effect of starting the experiment from conditioned populations at 20°C. Therefore, it is unlikely that laboratory acclimation to 20°C significantly influenced the results of the growth experiments. Each day, five to ten randomly selected individuals were isolated, and the number of setigerous segments was counted. They were then returned to the bowl. I found no difference in worm length *versus* number of setigerous segments for the three populations (Fig. 1). I therefore assume that my measure is an homogeneous indicator of growth over all populations. From these data, I determined a
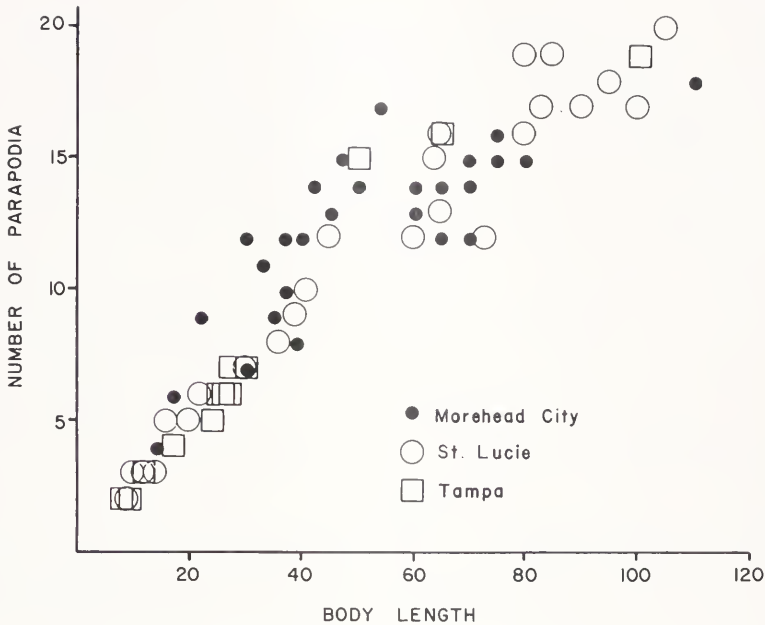
FIGURE 1.   Body length (mm) *versus* number of setigerous segments for the two Florida populations of *O. macrovifera* (Tampa and St. Lucie Inlet) and the North Carolina population of *O. costlowi*.

somatic growth rate by regression analysis of setigers on time. Difference in growth rates within and between populations was evaluated using standard analyses of variance related to regression (Sokal and Rohlf, 1981).

Second, newly emerged juveniles were placed separately (and arranged randomly) in 1 ml wells of glass spot plates, and provided with sea water and spinach. After seven days, the number of setigerous segments was counted for each individual, which permitted comparisons between populations via nested analysis of variance. This experiment was performed at 25°C only. These experiments were designed such that several families from each sibling species were employed; this permitted an estimate of variation in growth rate among families, that is, a full-sib analysis. All experiments were done after the field-collected populations had been maintained in the laboratory at room temperature (usually *ca.* 20°C) for one year (*ca.* 10 generations), in order to eliminate physiological characteristics that may have been fixed in the field. For this comparison, I employed North Carolina *O. costlowi* and St. Lucie's Inlet, Florida *O. macrovifera*.

Egg diameter was measured with an ocular micrometer fitted to a Wild dissecting microscope (at 50×). I also recorded the time and number of setigers corresponding to the acquisition of adult jaws. Finally, the number of eggs per case was counted. Life history characteristics of two populations of *O. macrovifera* were compared. Although geographically separated, these two populations were completely interfertile.

An energy budget model of growth rate

A simple model based upon energy budgets may be used to predict genetic differences between North Carolina and Florida sibling species. Imagine the presence of cold- and warm-adapted genotypes. Figure 2 shows a hypothetical difference between
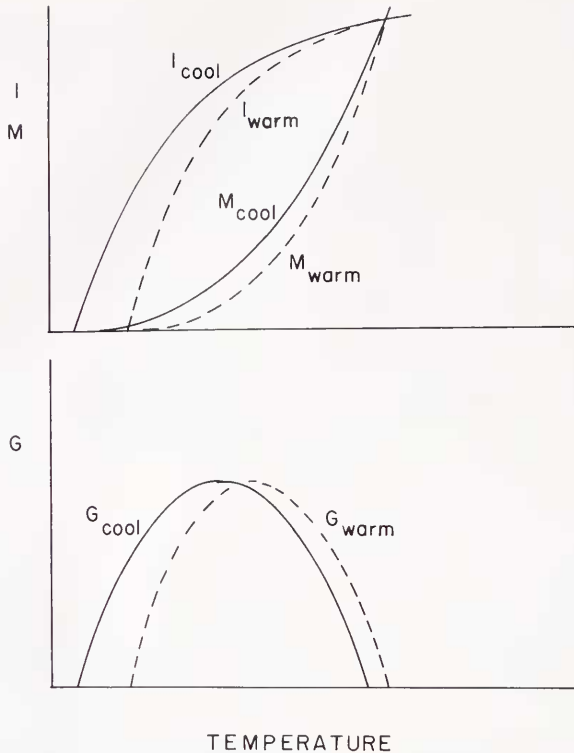
FIGURE 2. Graphical model explaining differential adaptation among latitudinally separated populations. Top diagram: Rate of ingestion, I, and metabolic cost rate, M, is illustrated for two hypothetical populations living in different thermal regimes. The regimes have similar maximum but differing minimum temperatures. Lower diagram: Difference between I and M curves yields reserves available for growth, G. The maximum growth rate of the warm-adapted form is displaced, relative to the cold-adapted form, towards higher temperature.

the two genotypes in energy acquired *versus* metabolic expenditure as a function of increasing temperature. The two hypothetical genotypes differ in that the energy intake and metabolic expenditure curves are displaced from each other such that the cold-adapted genotype enjoys a growth advantage at lower temperature (Fig. 2b).

This model predicts that at lower temperature, the cold-adapted form should grow more rapidly than the warm-adapted form. As temperature increases, this difference should diminish to a zero point, beyond which the warm-adapted genotype should enjoy the advantage. This advantage may simply involve relatively rapid growth. If the warm-adapted genotype lives in temperatures never experienced by the cold-adapted form, then the cold-evolved form might die at higher temperature, due to an excess of metabolic cost relative to rate of gained energy. Thus, the differential growth among individuals adapted to different temperatures would be seen only in the lower part of the temperature scale.

RESULTS

Temperature at the sites

Seasonal differences in temperature at the three sampling localities differ more in the distribution of temperature and winter minima than in summer maxima (Fig.
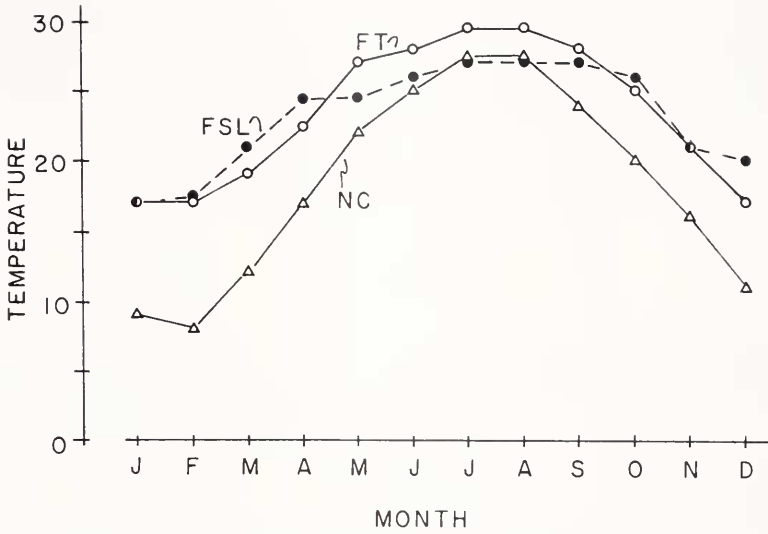
FIGURE 3. Mean monthly temperature of surface waters of the three localities: NC = Morehead City, North Carolina (actually nearby Beaufort, North Carolina); FSL = St. Lucie Inlet of Indian River, Florida; FT = Tampa Bay, Florida. Data derived from NOAA records.

3). Neither Florida locales experience mean monthly winter temperatures lower than 15°C. The North Carolina locale temperature surpasses 25°C for only two months, while both Florida sites are above 25°C for 5–6 months.

Whole family analyses

Figure 4 demonstrates the nature of the data obtained for somatic growth estimated for a given family (the complete data set is available upon request from the author). Growth rate was relatively uniform at 20, 25, and 30°C, but quite variable among individuals at 15°C.

Table I summarizes the variance analysis of the family growth regression on time, when comparing combined Florida locales with the North Carolina locale. At 15, 20, and 25°C, somatic growth rate of North Carolina animals surpasses that of Florida animals ($P < .001$). At 30°C, growth rates are approximately equal. The ratio of growth rate of North Carolina:Florida animals diminishes progressively from 15°C (1.58) to 30°C (1.02). The absolute difference in growth rate, however, is greatest at the two intermediate temperatures.

Significant differences between Florida populations were found at 15°C ($P < .001$) and 25°C ($P < .05$) (Table II). The magnitude of difference, however, is great only at 15°C, as demonstrated by the ratio of somatic growth rates at the four temperatures. At 15°C, growth differed between the two populations by a surprising factor of *ca.* 2. The variance analysis (Table III) also demonstrates that, for a given site and temperature, among-family growth rates were significantly different within sample populations from all three source localities. A more appropriate experimental design would spread members of the same family among different temperature treatments to estimate the family variance component. This approach is taken in the companion paper on intraspecific latitudinal differences (Levinton and Monahan, 1983).
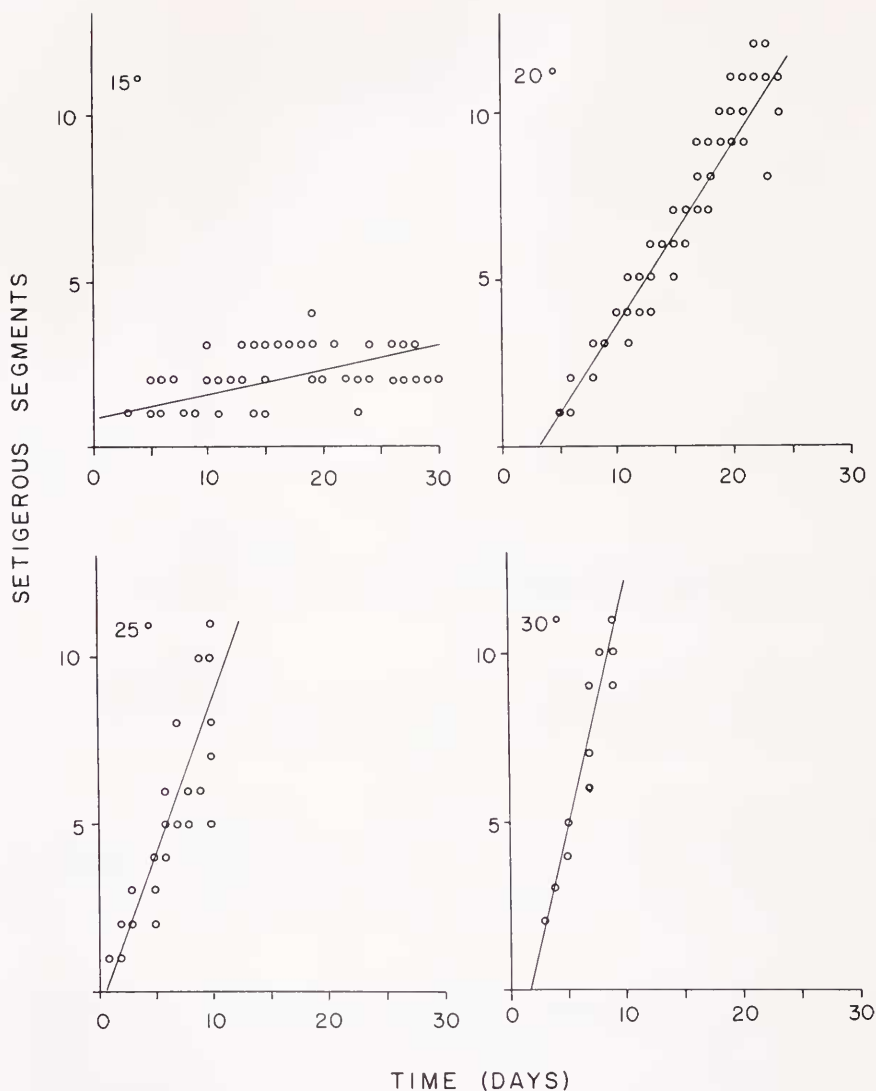
FIGURE 4.   Examples of growth regressions of families of *O. costlowi* run at 15, 20, 25, and 30°C.

Survivorship of families

    Eleven families each from North Carolina and the combined Florida locales were run at 30°C. The survival (defined as greater than 20 percent survival of individuals) of families from the combined Florida locales was much greater (10 out of 11) than that of the North Carolina site (1 out of 11). This difference in survival is significant ($P = .01$; 2 × 2 contingency table; Fisher's Exact Test). At lower temperatures survival was very high and similar between the two areas. The high mortality at 30°C in the North Carolina samples was surprising, in light of the rapid growth observed up to the day that death was observed, usually near the time of sexual maturity. Referring

Growth differences and variance analysis of regression statistics relating setigers to time

Experimental temperature	F_s	Degrees of freedom	Growth rate:		P	R
			Florida	North Carolina		
15	12.85	917	0.041	0.065	<.001	1.58
20	154.37	1732	0.364	0.520	<.001	1.43
25	41.99	962	0.853	0.956	<.001	1.12
30	1.58	828	1.215	1.243	NS	1.02

NS = not significant.

F statistic measures among-family *versus* between-locality variance of growth rate. Florida localities (*O. macrovifera*) are pooled for comparison with North Carolina (*O. costlowi*) locality. R = ratio of North Carolina to Florida growth rate (in setigerous segments/day).

to Figure 3, it is apparent that 30°C is greater than the mean monthly temperature experienced by all three populations. The data, however, probably underestimate the temperature achieved in the shallow microhabitats occupied by the worms. The Tampa site experiences the greatest summer maximum mean temperature.

Growth of individuals

Growth of North Carolina *O. costlowi* was found to be greater than that of Florida (St. Lucie) *O. macrovifera* (Table IV). Additionally, growth rate differed significantly among families. It is not known whether this difference can be attributed to genetic differences or to maternal effects (now under investigation). In both source populations, among-family differences were strongly significant ($P < .001$). These data indicate that among-family differences must be accounted for in physiological experimentation.

Life-history differences

Significant differences were found between the two Florida populations of *O. macrovifera,* despite complete interfertility between adults in crosses. Both egg size and number of setigerous segments at release (Table V) were larger in individuals from the Tampa population, relative to the St. Lucie population. Both eggs and larvae

TABLE II

Comparison of growth rates of O. macrovifera *populations from Tampa (Gulf Coast, Florida) and St. Lucie Inlet (Atlantic Coast, Florida)*

Experimental temperature	F_s	DF	Growth rate:		P	R
			Tampa	St. Lucie		
15	4.87	527	0.028	0.061	<.001	2.18
20	0.54	866	0.363	0.372	NS	1.02
25	6.31	702	0.842	0.799	<.05	0.95
30	0.19	538	1.149	1.136	NS	0.99

NS = Not Significant.

F statistic is a measure of among-family *versus* between locality variance. R = St. Lucie/Tampa growth rate.

TABLE III

Variance among families within the populations from each locality, at four temperatures

Temperature population	15°C			20°C			25°C			30°C		
	N	F	P	N	F	P	N	F	P	N	F	P
OCNC	5	5.61	<.001	11	22.32	<.001	5	6.68	<.001	7	17.86	<.001
OMT	5	32.76	<.001	5	16.76	<.001	5	9.56	<.001	5	8.71	<.001
OMSL	5	5.19	<.001	5	3.60	<.01	5	21.85	<.001	6	19.41	<.001

F statistic measures difference in variance within and among families from a given locality. (N = number of families; F = value of F statistic, P = significance level for among-family heterogeneity in somatic growth rate (setigerous segments/day)). OCNC = *O. costlowi*, North Carolina; OMT = *O. macrovifera*, Tampa; OMSL = *O. macrovifera*, St. Lucie Inlet.

of North Carolina *O. costlowi* were smaller than the eggs and larvae of Florida populations of *O. macrovifera*. The size at which the adult jaw developed was greater in *O. macrovifera* (Table V). Akesson (1978) presents similar data, except for noting intraspecific variation in *O. macrovifera*.

DISCUSSION

These results are consistent with an energy budget model that postulates a difference in adaptation of high and low latitude (*i.e.*, thermally differing) populations. The northern *O. costlowi* shows greater somatic growth rate, but this advantage decreases with increasing temperature as predicted by the model. At 30°C, the difference is nonexistent and North Carolina families show very high mortality. The rich food (spinach) used in the experiments may have tended to shift the growth differences, favoring growth of the northern populations at higher temperatures than found under field conditions with a food supply of lower nutritional content. Such an effect was documented by Bayne *et al.* (1973) in the energy budget of the mussel, *Mytilus edulis*. The rich food provided in the present experiments might explain the rapid growth observed at 30°C for all three populations. A poorer food that is available in nature might not permit a favorable energetic balance at this extreme temperature.

As illustrated by Figure 3, the thermal regimes at the three localities do not differ

TABLE IV

Analysis of variance for growth rates of individuals distributed among nine families each for O. costlowi *from Morehead City, North Carolina and* O. macrovifera *from St. Lucie's Inlet, Florida*

O. costlowi, North Carolina: Total growth = 7.48 + .37 (95% CL)

Source of Variation	df	MS	F_s
Among Families	8	15.08	9.40***
Within Families	72	1.60	

O. macrovifera, Florida: Total growth = 5.52 + .23 (95% CL)

Source of Variation	df	MS	F_s
Among Families	8	4.42	5.79***
Within Families	72	0.76	

*** $P < .001$.

Growth is measured as number of setigerous segments added in seven days after hatching.

TABLE V

Some differences in life histories between O. costlowi *for Morehead City, North Carolina, and O.* macrovifera *from St. Lucie Inlet (Atlantic Coast of Florida) and Tampa (Gulf Coast of Florida)*

		O. macrovifera	
Characteristic	*O. costlowi*	Tampa	St. Lucie
Egg Diameter (μm)	104.4 + 9.85 (225)	134.2 + 17.42 (128)	145.5 ± 16.84 (80)
Setigerous Segments When Hatching	0 ± 0 (100)	1.5 ± 0.74 (170)	2.6 ± 0.68
Acquisition of Adult Jaws (Males)	11.4 ± 0.91 (39)	14.8 ± 0.75 (12)	—
Acquisition of Adult Jaws (Females)	13.5 ± 0.93 (44)	16.1 ± 0.64 (18)	—

Sample size (in parentheses) and standard deviations are given.

very much in maximum summer temperature. The most important difference lies in the seasonal distribution of temperature and the winter minimum. The Florida locales have winter minima near 15°C, which is substantially greater than for North Carolina. Increasing the experimental temperature from 15 to 30°C provides an opportunity for increasing growth rate (Fig. 3). In the lower range, the high latitude population enjoys the advantage in growth efficiency. At 30°C, however, the two sibling species do not differ in growth, although North Carolina *O. costlowi* suffer high mortality. This may stem from an inability to acclimate and a predetermined pattern of investment of energy for somatic growth, despite the cost in maintenance.

At present, there are no data on reproductive output as a function of temperature. It is likely that reproductive investment will follow the patterns found for somatic growth. Akesson (1976) investigated the effect of temperature on the life cycle of *O. labronica* and demonstrated optimum intermediate temperatures for eggs per egg mass and egg output per female per day. In the sequential hermaphrodite, *Ophryotrocha puerilis,* the size at which sex change from male to female occurs is greater in a northern (Atlantic) subspecies, relative to a southern (Mediterranean) subspecies (Sella, 1978). Sella (1980) has presented evidence that the size at sex change in *O. puerilis* is genetically regulated and maintained by stabilizing selection. This suggests that thermal limitations may influence the life history patterns of sequential hermaphrodites much as spatially varying mortality patterns can (*e.g.,* Charnov, 1978, 1979, 1981). Although the northern subspecies of *O. puerilis* switches sex at a larger number of segments, individuals grow to this size in the same number of days as individuals of the southern subspecies, implying accelerated growth for the northern form. This result is consistent with the present findings. Further work on these subspecies demonstrates intraspecific differentiation in growth rates comparable to the interspecific data presented here (Levinton and Monahan, 1983).

These results suggest that, given the strong differences in temperature along the eastern coast of North America, some compensation is possible for life at low temperature. The model and results also suggest that populations evolve locally to maximize growth rate. It is therefore incorrect to state, for example, that southern (high temperature) populations evolve slower growth rates, relative to northern populations. Rather, all populations are adapted for maximum growth rate, and they sacrifice

efficiency at temperatures rarely experienced to maximize growth efficiency at temperatures that are experienced commonly. Thus southern individuals grow more slowly at lower temperature because evolution has shifted the metabolism-temperature relationship to minimize metabolic cost at high temperature; this shift, however, restricts activity and growth at low temperature, relative to higher latitude forms. Bervan *et al.* (1978) developed a temperature-related explanation for growth differences in salamanders living at different altitudes. They described the necessary compensation of living in cold climates as "countergradient selection," implying that selection for increased growth rate works against the limiting effects of cold temperatures on poikilotherms. But animals in warm climates have their problems as well; genetic variance for a favorable metabolism-temperature response would therefore be of great advantage, given a geographic/altitudinal gradient of temperature.

Newell and Kofoed (1977) demonstrate that thermal constraints can be met with compensation via physiological acclimation. Thus the presumed genetic component we observe here must be placed aside this non-genetic response in any accounting of response to the thermal regime. The ability to acclimate is just as much an evolutionary response as the differences in growth we have discussed.

Growth experiments performed in this study were done on individuals from different populations, reared under the same laboratory conditions. Assuming laboratory conditions are reasonably related to field conditions, these results suggest that the growth differences are genetic, and confirm the expectation that populations of coastal invertebrates show strong regional differentiation in physiologically important characters (Battaglia, 1959; Gooch and Schopf, 1971; Levinton and Fundiller, 1975). These results suggest that an integrated study of energy budgets, genetics, and somatic growth rates will be useful in understanding regional differentiation within marine species. As the differences found in this study lasted (apparently) for *ca.* 10 generations of laboratory rearing (as in Battaglia, 1959), one can be reasonably certain that environmental effects can be ruled out.

LITERATURE CITED

Akesson, B. 1976. Temperature and life cycle in *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Ophelia* 15: 37–47.

Akesson, B. 1978. A new *Ophryotrocha* species of the *Labronica* group revealed in crossbreeding experiments. Pp. 573–590 in *Marine Organisms: Genetics, Ecology, and Evolution*, B. Battaglia and J. L. Beardmore, eds. Plenum Publ. Co., New York.

Ament, A. 1979. Geographic variation in relation to life history in three species of the marine gastropod

genus *Crepidula:* growth rates of newly hatched larvae and juveniles. Pp. 61–76 in *Reproductive Ecology of Marine Invertebrates,* S. E. Stancyk, ed. Univ. of South Carolina Press, Columbia, SC.

BATTAGLIA, B. 1959. Ecological differentiation and incipient intraspecific isolation in marine copepods. *Ann. Biol.* **33:** 259–268.

BAYNE, B. L., R. J. THOMPSON, AND J. WIDDOWS. 1973. Some effects of temperature and food on the rate of oxygen consumption by *Mytilus edulis* L. Pp. 181–193 in *Effects of Temperature on Ectothermic Organisms,* W. Wieser, ed. Springer-Verlag, New York.

BERVAN, K. A., D. E. GILL, AND S. J. SMITH-GILL. 1979. Countergradient selection in the green frog, *Rana clamitans. Evolution* **33:** 609–623.

BURTON, R. S., AND M. W. FELDMAN. 1983. Physiological effects of an allozyme polymorphism: glutamate-pyruvate transaminase and response to hyperosmotic stress in the copepod *Tigriopus californicus. Biochem. Genet.* **21:** 239–251.

CHARNOV, E. L. 1978. Sex ratio: adaptive response to population fluctuations in pandalid shrimp. *Science* **200:** 204–206.

CHARNOV, E. L. 1979. Natural selection and sex change in pandalid shrimp: test of a life-history theory. *Am. Nat.* **113:** 715–734.

CHARNOV, E. L. 1981. Sex reversal in *Pandalus borealis:* effect of a shrimp fishery. *Mar. Biol. Lett.* **2:** 53–57.

CONOVER, D. O., AND B. E. KYNARD. 1981. Evolution of sex determination: interaction of temperature and genotype in a fish. *Science* **213:** 577–579.

DEHNEL, P. A. 1956. Growth rates in latitudinally and vertically separated populations of *Mytilus californianus. Biol. Bull.* **110:** 43–53.

FOX, H. M. 1936. The activity and metabolism of poikilothermal animals in different latitudes. *Proc. Zool. Soc. Lond.* **106:** 945–955.

GIBSON, M. B. 1954. Upper lethal temperature relations of the guppy, *Lebistes reticulatus. Can. J. Zool.* **32:** 393–407.

GOSLING, E. 1979. Hidden genetic variability in two populations of a marine mussel. *Nature* **279:** 713–715.

GOOCH, J. L., AND T. J. M. SCHOPF. 1971. Genetic variation in the marine ectoproct *Schizoporella errata. Biol. Bull.* **141:** 235–246.

HALL, J. G. 1983. *Temperature-related Catalytic Differentiation Among Homologues of Glucosephosphate Isomerase (EC 5.3.1.9) Isolated From the Bivalves* Mytilus edulis *and* Isognomon alatus. PhD. Dissertation, State University of New York at Stony Brook.

HOCHACHKA, P. W., AND G. N. SOMERO. 1973. *Strategies of Biochemical Adaptation.* W. B. Saunders, Philadelphia.

JOHNSON, A. G., AND F. M. UTTER. 1973. Electrophoretic variants of aspartate aminotransferase of the bay mussel, *Mytilus edulis* (Linnaeus, 1758). *Comp. Biochem. Physiol.* **44B:** 317–323.

KINNE, O. 1962. Irreversible non-genetic adaptation. *Comp. Biochem. Physiol.* **5:** 265–282.

KINNE, O. 1964. Non-genetic adaptation to temperature and salinity. *Helgol. Wiss. Meeresunters.* **10:** 433–458.

KOEHN, R. K., R. MILKMAN, AND J. B. MITTON. 1976. Population genetics of marine pelecypods. IV. Selection, migration and genetic differentiation in the blue mussel, *Mytilus edulis. Evolution* **30:** 2–32.

KOEHN, R. K., R. I. E. NEWELL, AND F. IMMERMAN. 1980. Maintenance of an aminopeptidase allele frequency cline by natural selection. *Proc. Nat. Acad. Sci. USA* **9:** 5385–5389.

KROGH, A. 1916. *Respiratory Exchange of Animals and Man.* Longmans Green, London.

LEVINTON, J. S., AND D. L. FUNDILLER. 1975. An ecological and physiological approach to the study of biochemical polymorphisms. Pp. 165–178 in *Proc. 9th Europ. Mar. Biol. Symp.,* H. Barnes, ed. Aberdeen University Press, Aberdeen, Scotland.

LEVINTON, J. S., AND H. H. LASSEN. 1978. Selection, ecology, and evolutionary adjustment within bivalve mollusc populations. *Phil. Trans. Roy. Soc. Lond. B* **284:** 403–415.

LEVINTON, J. S., AND R. K. MONAHAN. 1983. The latitudinal compensation hypothesis: growth data and a model based upon energy budgets. II. Intraspecific comparisons between subspecies of *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). *Biol. Bull.* **165:** 699–707.

LEVINTON, J. S., AND T. H. SUCHANEK. 1978. Geographic variation, niche breadth, and genetic differentiation at different geographic scales in the mussels *Mytilus californianus* and *Mytilus edulis. Mar. Biol.* **49:** 363–375.

LOOSANOFF, V. L., AND C. A. NOMEJKO. 1951. Existence of physiologically different races of oysters, *Crassostrea virginica. Biol. Bull.* **101:** 151–156.

MANGUM, C. P. 1963. Studies on speciation in maldanid polychaetes of the North American Atlantic coast. III. Intra- and interspecific divergence in oxygen consumption. *Comp. Biochem. Physiol.* **10:** 335–349.

McLaren, I. A., C. J. Corkett, and E. J. Zillioux. 1969. Temperature adaptations of copepod eggs from the arctic to the tropics. *Biol. Bull.* **137**: 486–493.

Newell, R. C. 1973. Environmental factors affecting the acclimatory responses of ectotherms. Pp. 151–164 in *Effects of Temperature on Ectothermic Organisms,* W. Wieser, ed. Springer-Verlag, New York.

Newell, R. C., and L. H. Kofoed. 1977. Adjustment of the components of energy balance in the gastropod *Crepidula fornicata* in response to thermal acclimation. *Mar. Biol.* **44**: 275–286.

O'Gower, A. K., and P. I. Nicol. 1968. A latitudinal cline of haemoglobins in a bivalve mollusc. *Heredity* **23**: 485–491.

Pickens, P. E. 1965. Heart rate of mussels as a function of latitude, intertidal height, and acclimation temperature. *Physiol. Zool.* **38**: 390–405.

Rao, K. P. 1953. Rate of water propulsion in *Mytilus californianus* as a function of latitude. *Biol. Bull.* **104**: 171–181.

Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morphol.* **106**: 85–108.

Schneider, D. E. 1967. *An Evaluation of Temperature Adaptations in Latitudinally Separated Populations of the Xanthid Crab,* Rhithropanopeus harrisii *(Gould), by Laboratory Rearing Experiments.* PhD. Dissertation, Duke University.

Scholander, P. F., W. Flagg, V. Walters, and L. Irving. 1953. Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.* **26**: 67–93.

Sella, G. 1978. Responses adaptatives a differentes temperatures chez les deux sousespeces d'*Ophryotrocha puerilis,* pendant la phase male. *Cah. Biol. Mar.* **18**: 117–125.

Sella, G. 1980. The genetic system controlling the body length at which sex change occurs in *Ophryotrocha puerilis* (Annelida, Polichaeta). *Atti Soc. Toscana Sci. Nat. P. V. Mem. Ser. B* **87**: 197–203.

Sokal, R. R., and F. J. Rohlf. 1981. *Biometry.* W. H. Freeman and Company, San Francisco.

Somero, G. N., and A. L. DeVries. 1967. Temperature tolerance of some Antarctic fishes. *Science* **156**: 257–258.

Vernberg, W. B., and F. J. Vernberg. 1966. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca* V. Effect of temperature on tissue respiration. *Comp. Biochem. Physiol.* **17**: 118–126.

Weymouth, F. W., and H. C. McMillan. 1931. The relative growth and mortality of the Pacific razor clam (*Siliqua patula* Dixon) and their bearing on the commercial fishery. *Bull. U. S. Bur. Fish.* **46**: 543–567.

Williams, G. C., R. K. Koehn, and J. B. Mitton. 1973. Genetic differentiation without isolation in the American eel, *Anguilla rostrata. Evolution* **27**: 192–204.

Zamer, W. E., and C. P. Mangum. 1979. Irreversible non-genetic temperature adaptation of oxygen uptake in clones of the sea anemone *Haliplanella luciae* (Verrill). *Biol. Bull.* **157**: 536–547.

Zhirmunsky, A. V. 1959. The thermostability of actinias and their ciliated epithelium in natural conditions and in experimentally changed environmental temperatures. *Tsitologiya* **1**: 270–276 (In Russian).